PROMELOCRINUS FROM THE WENLOCK AT DUDLEY

by J. C. BROWER

ABSTRACT. Two melocrinitids occur in the Wenlock at Dudley. *Promelocrinus anglicus* Jaekel is represented by many specimens, whereas *Promelocrinus* sp. is only known from one partial fragment of the arms. Growth and variation have been studied in *P. anglicus*. Variation of number of plates in the interbrachial areas and in the ray trunks increases distally. The number of plates in a range of interbrachials is positively linked with the number of plates in adjacent ranges. However, the arm-branching parameters are mainly independent of one another. The earliest crinoids probably bear equal-sized arms in each ray with pinnules being present in the two outer arms but lacking in the two inner ones. Throughout subsequent development, the outer arms are unbranched although new brachials form and the length of the arms is augmented. The inner arms become hypertrophied into highly ramified ray trunks. The length of the ray trunk increases by the formation of new brachials and height increase of old plates. New ramules appear as new brachials are added to the ray trunk. Once the ramules are initiated, new brachials form at the distal tips of the growing ramules. Pinnules develop on the ramules and outer arms throughout growth. Lengths of old pinnules are augmented by the same mechanisms seen in the ramules and outer arms. The ontogeny of *P. anglicus* suggests that the acquisition of complexly ramified ray trunks results in unusually rapid rates of growth of new brachials and length of the arms. The rate of development is approximately squared relative to idealized crinoids with simple arm configurations. Unlike most crinoids, *P. anglicus* is characterized by isometry or positive allometry of the food-gathering system relative to tissue volume, so that the food-gathering ratios are either stabilized or increase throughout ontogeny. In *P. anglicus* and other melocrinitids, a complete filtration network is present which covers the entire perimeter of the arms, and almost all food particles flowing through the arms and pinnules would be filtered. Promelocrinids and melocrinitids were full mucus net feeders like most Recent adult crinoids.

MELOCRINITIDS and their allies represent one of the most diversified groups of Palaeozoic camerate crinoids, including about 120 species and subspecies, grouped in six genera. The evolution of melocrinitids has been described by Kirk (1929), Moore and Laudon (1943, pp. 89, 96–98), and Ubaghs (1953, pp. 710–712; 1958) and early forms were examined quantitatively by Brower (1973, pp. 432–437). The ancestral glyptocrinids are characterized by two unbranched arms in each ray and a filtration network with large gaps. The first step in evolution was the acquisition of four arms per ray. Subsequently, the inner arms of each ray became hypertrophied into highly ramified ray trunks while the outer arms were reduced and eventually lost in order to provide room for the ray trunks. This process increases the food-gathering capacity as well as forming a complete filtration net which completely filters the water in the vicinity of the crinoid. The general tendency is to increase the body size of adult crinoids throughout the lineage. The concomitant evolution of increased size and food-gathering capacity is suggestive of size-related allometry.

While engaged in a numerical study of the evolution of melocrinitids (Brower, in press) it was noticed that the British forms had never been fully described. Consequently the purpose of this paper is to present systematic descriptions of the melocrinitids from the Wenlock at Dudley, and in particular, to study growth and variation in *Promelocrinus anglicus* Jaekel.

TERMINOLOGY

Generally, the terminology follows that of Moore (1952, text-fig. 18-2). The proximal plate of the camerate *CD* (posterior) interray is designated primanal (Jaekel 1918, p. 28). Brachials rigidly incorporated into the calyx are termed fixed-brachials. The ray-orientation system is that of Carpenter (1884, text-fig. 2).

The camerate crinoids examined here have two to four free arms in each ray. Two-armed species show two half-rays; the area between these and the equivalent position in four-armed crinoids is termed an intersecundibrachial area, the calyx plates of which are intersecundibrachs. In four-armed taxa, two half-rays are present, each consisting of two free arms called quarter-rays. The space between two quarter-rays contains the intertertibrachs. All plates located between the rays are interbrachials. The camerate plate sequence directly overlying the primanal is the anal series, the elements of which are anal-series plates. The anal series is generally separated from the *C* and *D* rays by *CD* interray interbrachials.

Promelocrinids have four arms in each ray. The inner arms are hypertrophied into ray trunks which consist of uniserial nonpinnulate brachials. Pinnulate ramules are located along the ray trunks. The outer arms remain unbranched (see text-fig. 2*a* and *c* for illustration of terms).

SYSTEMATIC PALAEONTOLOGY

Subclass CAMERATA Wachsmuth and Springer, 1885
Order MONOBATHRIDA Moore and Laudon, 1943
Suborder GLYPTOCRININA Moore, 1952
Superfamily MELOCRINITICAE Ubaghs, 1953
Family MELOCRINITIDAE Zittel, 1878
PROMELOCRINUS Jaekel, 1902

Type species. By monotypy. *Promelocrinus anglicus* Jaekel, 1902, p. 1068, fig. 8. Ubaghs (1958, pp. 267–304) gives a detailed discussion of *Promelocrinus* and its nomenclature.

Promelocrinus anglicus Jaekel

Plates 100, 101; Plate 102, figs. 1, 2, 4.

1873 *Mariacrinus flabellatus* Salter, 1873, p. 122.
1891 *Melocrinus flabellatus* (Salter), Woods, p. 41.
1902 *Promelocrinus anglicus* Jaekel, p. 1068, fig. 8.
1926 *Melocrinus? spectabilis* Angelin, Springer, p. 27, pl. 5, figs. 2, 3.
1926 *Mariacrinus* sp. Springer, p. 29, pl. 5, fig. 13.
1943 *Melocrinites spectabilis* (Angelin), Bassler and Moodey, *pars*, p. 559.
1943 *Promelocrinus anglicus* Jaekel, Bassler and Moodey, p. 652.
1953 *Promelocrinus anglicus* Jaekel, Ubaghs, p. 711, fig. 82*c*.
1958 *Promelocrinus anglicus* Jaekel, Ubaghs, p. 300, text-fig. 18.
1973 *Promelocrinus anglicus* Jaekel, Webster, p. 224.
1973 *Promelocrinus anglicus* Jaekel, Brower, p. 432, text-fig. 36.

Holotype. Unnumbered specimen in the Paläontologisches Museum, Museum für Naturkunde, Berlin, DDR, 104. A poorly preserved crown on a small slab.

Other material. P. anglicus is a moderately abundant crinoid in the Dudley Limestone and I have examined approximately fifty specimens of type and nontype material. Syntypes of *Mariacrinus flabellatus* Salter: SM. (Sedgwick Museum) A10136, a crown and three stem segments; A12753–12758, partial crowns. Specimens figured by Springer (1926, pl. 5, figs. 2, 3) as *Melocrinus? spectabilis* Angelin: S. (Springer Collection at United States National Museum) 270. Young crown illustrated by Springer (1926, pl. 5, fig. 13) as *Mariacrinus* sp.: S. 270. Specimens figured by Ubaghs (1958, text-fig. 18) as *P. anglicus* Jaekel: SM. 12767; BMNH. (British Museum of Natural History) E26497. Specimen mentioned by Ubaghs (1958, p. 269) as

P. anglicus: BMNH. 57105. Specimens figured herein as *P. anglicus*: SM. A10136, A12767; GSM. (Geological Survey Museum) 85098, 91770, 103737; BMNH. E26498, 36848; S. 270, 271. In addition, two unidentified rooting devices are illustrated: SM. A12759, A12761. Material examined but undescribed in this paper includes SM. A36644, several specimens in A10136, A12768, A12769. GSM. 103738–103743. BMNH. 25514, 40123, 40328, 47931, 57132–57135. Several specimens in S. 270, two unnumbered specimens in the Springer Collection. UB. (University of Birmingham), Holcroft Collection 2, 260, 287, 309, 506, 511; Ketley Collection 42, 99, 112, 122. DM. (Dudley Museum) 407–412. YM. (York Museum) JCB. 74/1, 74/2.

Unidentified roots. SM. A12759–12762, A12764–12766. Salter referred a series of massive cirrus roots to this species for unknown reasons. Inasmuch as there are no known calyces of *P. anglicus* which possess this type of rooting device, no direct reason exists to assign these roots to *P. anglicus*. Possibly Salter considered the roots and crowns conspecific because they were closely associated when the specimens were originally purchased. However, this is not supported by the available material, or by any notes made by Salter, and the roots are regarded here as unidentified.

Type locality. Silurian, Wenlock. Dudley Limestone, near Dudley, West Midlands. The exact locality is unknown. The specimens were found during the last century by quarrymen, children, and other collectors. The typical locality label simply reads 'Dudley'. The Wrens Nest is the most extensively quarried of the Silurian inliers near Dudley.

Diagnosis. A large species of *Promelocrinus* with calyx heights ranging up to about 42 mm. Numerous ramules present and the ray trunks of adults bear twelve to fifteen ramules. Adult crinoids possess biserial brachials. Calyx ornamentation variable; median-ray ridges present but these may be strongly or weakly developed; surfaces of plates sometimes smooth but usually finely granulose; aside from the median-ray ridges, the plates may be flat or somewhat swollen and nodose; a few specimens have fine multiple stellate ridges.
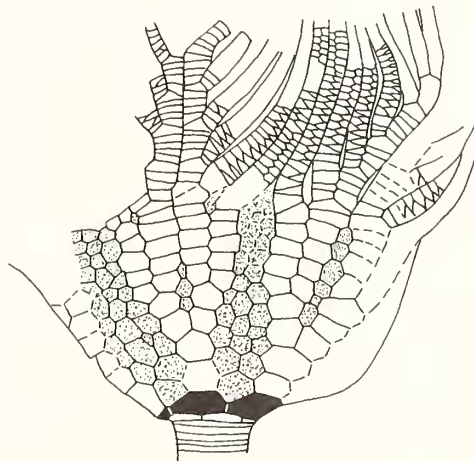
TEXT-FIG. 1. Holotype of *Promelocrinus anglicus* Jaekel. Lateral view of poorly preserved crown, ×2·2. Symbols: radials—black; interbrachs, intersecundibrachs, and intertertibrachs—stippled.

Description of adult. Young specimens are described in the ontogeny section. Calyx conical, generally with slightly rounded walls, height/width ratio of uncrushed specimens about 0·8. Ornamentation variable; median-ray ridges present but range from weakly to strongly developed; surfaces of plates generally covered with fine irregular granules although some smooth examples are known; aside from plates with median-ray ridges, the plates may be smooth or somewhat swollen and nodose; several examples show fine multiple stellate ridges.

Basals four, one large and three small, large basal with sutures in *B* and *E* ray positions; small basals pentagonal, height/width ratio ranges from 0·3 to 0·6; large basal six-sided, with distal margin truncated
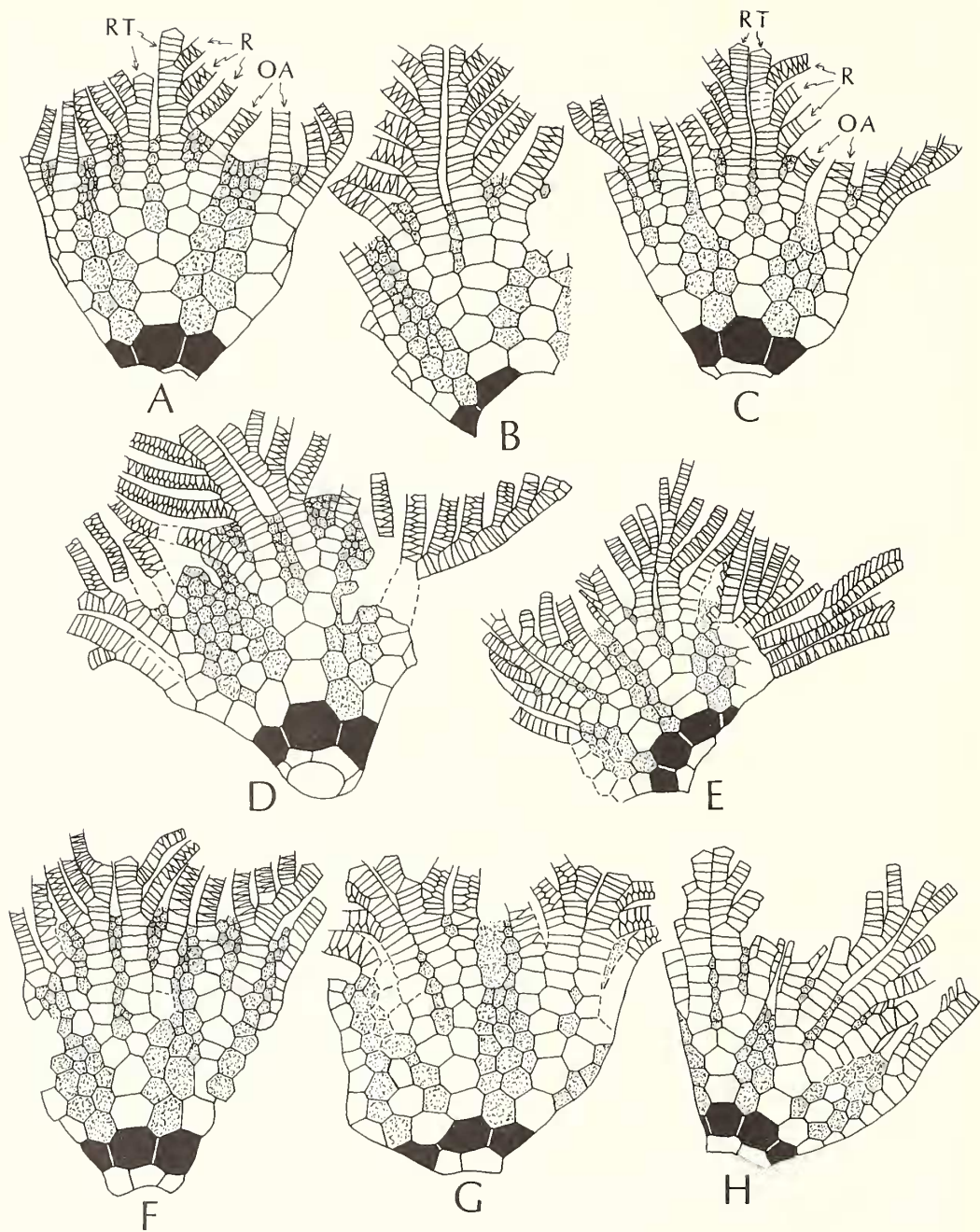
for reception of radial, height/width ratio 0·3. Radials largest plates in calyx, hexagonal, in lateral contact in all interrays; height/width ratio varies from 0·8 to 1·0. Primibrachs slightly smaller than radials. Primibrach *1* hexagonal, height/width ratio from 0·7 to 1·0. Primibrach *2* axillary, bearing proximal secundibrachs, septagonal, height/width ratio from 0·8 to 1·0. Secundibrachs generally two per ray; rarely one or three plates are present. Secundibrach *1* hexagonal with inner sides joined; height/width ratio varies from 0·6 to 0·9. Secundibrach *2* axillary, bearing proximal tertibrachs of ray trunks and outer arms; secundibrach *2* varies from pentagonal to septagonal although six- and seven-sided plates are most common; height/width ratio ranges from 0·5 to 1·0. Lower portion of ray trunk ranging up to the proximal quartibrachs and several brachials of the first ramule are fixed into the calyx by intersecundibrachs and intertertibrachs; usually six tertibrachs are present, uniserial, lacking pinnules; shapes of nonaxillary plates ranging from four- to seven-sided, plates becoming shorter in distal direction, axillary tertibrach pentagonal or septagonal; proximal quartibrachs similar to tertibrachs except for smaller size. Six or seven tertibrachs of the outer arm fixed into calyx by interbrachs and intertertibrachs; plates like tertibrachs of ray trunks except that traces of fixed pinnules are often seen, such as on the interray side of tertibrach *2*. Interbrachial areas consist of about eleven to thirteen ranges of plates; proximal plates large and regular, becoming smaller and less regular distally; approximately five ranges of plates located below tertibrach *1* of the outer arms; interbrachial areas reach maximum width at primaxil, then become constricted above secundiaxil (see section on variation for details of plate formulae and the intersecundibrachs). Intertertibrachs small and irregular, one plate in proximal range, distal ranges consisting of one or two plates each. Primanal located between the proximal primibrachs of the *C* and *D* rays; primanal followed by three plates, the central of which is the proximal anal series plate and the two flanking ones are *CD* interray interbrachs. Anal series plates generally hexagonal; from two to five plates present, above which the anal series plates cannot be separated from interbrachs of the *CD* interray. Proximal range of *CD* interray interbrachs consists of one plate, higher ranges with one or two plates; above the level of the anal series, the *CD* interray interbrachials merge, and form ranges of three to five plates.

Full discussion of the arms is given in the sections on variation and ontogeny. Ray trunk brachials uniserial, nonpinnulate, much wider than high, nonaxillary plates roughly rectangular, axillary plates five-sided. Within a single series of plates, the proximal ones are narrowest but these expand distally so that the axillary is the widest plate in the series (text-fig. *3j–l*); this ensures that the axillary gives rise to large ramule and ray trunk brachials which is required by problems of supporting the food-gathering system. Proximal brachials of ramules and outer arms uniserial but more distal brachials are pinnulate and of immature or mature biserial type. Immature biserial brachials have curved proximal and distal margins which converge on each other so that the brachials appear wedge-shaped, pinnule facets protuberant (text-fig. *3c–g*). Mature biserial brachials are found in the proximal parts of ramules of several specimens; proximal and distal margins parallel to one another; inner margins sharply separated from proximal and distal ones, converging on each other; pinnule facets less protuberant than those of immature biserial brachials (text-fig. *3h, k*). Well-preserved brachials show finely crenulate sutures (text-fig. *3g, h, k, l*); these are not seen on weathered brachials which appear to have straight sutures. Pinnules long, slender; mature ones consist of ten or more elongate pinnulars; pinnulars with two rows of irregular covering plates (text-fig. *3e, f, i*).

TEXT-FIG. 2. Calyces of *Promelocrinus anglicus* Jaekel. A, lateral view of SM. A12767, note relatively slender arms and complete intersecundibrachial areas, × 1·5. B, *D* ray view of S. 270, specimen identified by Springer (1926, pl. 5, fig. 3) as *Melocrinus? spectabilis* Angelin, the intersecundibrachial areas are complete, × 1·8. C, lateral view of GSM. 85098, a crown with interbrachial areas that are constricted at the level of the secundibrachs and proximal tertibrachs, × 1·6. D, *C* ray view of GSM. 91770, note complete intersecundibrachial areas with two plates in most ranges, × 1·6. E, lateral view of BMNH. 38648, an immature calyx, × 2·4. F, lateral view of GSM. 103737, an adult crown with complete intersecundibrachial areas, × 1·4. G, probably *C* ray view, SM. A10136, a syntype of *Mariacrinus flabellatus* Salter, note partially developed intersecundibrachial areas in which the inner arms are joined together in areas which lack intersecundibrachs, × 1·0. H, possibly *D* ray view, BMNH. E26498, a young crinoid with complete intersecundibrachial areas, × 2·6. Symbols: radials—black; interbrachials, intersecundibrachs, and intertertibrachs—stippled; in A and C, RT, R, and OA denote the ray trunks, ramules, and outer arms respectively.

E

Only proximal portion of column known, round, heteromorphic; column consists of five orders of plates, one order of nodals (N), and four orders of internodals (IN); proximal noditaxis complete except that 4IN are lacking; 4IN is completely developed in third or fourth noditaxis below the calyx; all plates with nodose margins except 4IN. Articular surfaces of columnals partly known; axial canal pentalobate, with lobes pointing toward the interrays as usual for monocyclic crinoids.

Variation in interbrachial areas. Promelocrinus anglicus is known from a relatively large sample consisting of about fifty specimens which allows some aspects of variation to be examined. Although there are numerous abundant species of Palaeozoic crinoids, studies of variation are surprisingly rare. Consequently, it is difficult to establish exactly how conservative are some of the basic characters that have been used in crinoid taxonomy for many years. Hopefully this study will provide some information about the interbrachial areas and arm-branching patterns of melo-crinitids.

The structure of the primibrachs and the interbrachs was studied on thirty-five specimens, each of which is represented by a single data set. Most crinoids are not well enough preserved so that more than one ray and interray area can be determined. Consequently, the data only reflect variation between specimens and no information is available on variation within individuals. Owing to preservation, it is usually not possible to make complete sets of measurements on most crinoids. Most data come from the proximal parts of the rays and interbrachial areas.

The shapes of the primibrachs were seen in thirty-five specimens. Primibrach *1* is invariably hexagonal; septagonal outlines are observed on thirty-four axillary primi-brachs while one plate is pentagonal. These figures show low variation and demon-strate that the shapes of these plates are largely stabilized. *Alisocrinus tetrarmatus* Brower, a primitive Ordovician melocrinitid, is characterized by greater variability (Brower 1973, p. 430).

To a large extent, all of the interbrachial areas are subject to similar variation and consequently, the interbrachs between the rays are emphasized and the other areas only briefly discussed.

The parameter measured is the number of plates in the different ranges of inter-brachials. The following trends of variation are shown by the statistics in Tables 1

TABLE 1. Table showing variation of interbrachs.

Number of range (numbers increase from proximal to distal ranges of plates)	Mean number of interbrachs in listed range	Standard deviation	Percentage standard deviation [(standard deviation/ mean) × 100]	Range	Number of specimens
1	1·00	0·0	0·0	—	29
2	2·00	0·0	0·0	—	29
3	2·78	0·424	15·2	2·0–3·0	27
4	2·90	0·417	14·3	2·0–4·0	24
5	3·02	0·602	19·9	2·0–4·0	21
6	3·13	0·663	21·2	2·0–4·0	19
7	3·03	0·562	18·5	2·0–4·0	16
8	2·93	0·730	24·9	2·0–4·0	14
9	2·89	0·650	22·5	2·0–4·0	9
10	3·50	1·12	31·9	3·0–5·5	5
11	3·50	1·12	31·9	3·0–5·5	5

TABLE 2. Correlation matrix for the interbrachs. (All correlation coefficients are significant at the 0·01 risk level.)

Position of interbrachial range (numbers increasing distally)	1·00	0·798	0·934	0·930
Number of interbrachs in the various ranges	0·798	1·00	0·881	0·904
Standard deviation	0·934	0·881	1·00	0·988
Percentage standard deviation	0·930	0·904	0·988	1·00

and 2. All characters are positively correlated. Proceeding from proximal to distal ranges, the average number of plates increases from 1·0 to 3·5, the standard deviations rise from nil to 1·12, and the percentage standard deviations range from nil to 32%. This theme of distally increasing number of plates and variation seems to be characteristic of most Paleozoic camerate crinoids with numerous fixed-brachs (e.g. Brower 1973, 1974). A correlation matrix was computed for the number of plates within the various ranges of interbrachs. The proximal two ranges of plates are invariant so all correlations involving these are nil. For the higher ranges, most of the significant coefficients (0·05 risk level) lie close to the diagonal of the matrix. This indicates that the number of interbrachs in a particular range is best correlated with those of the adjacent one or two ranges of plates rather than the number of plates in all ranges. The significant correlations are all positive and these vary from 0·40 to 0·96.

P. anglicus exhibits three types of intersecundibrachial areas: 1, fully developed in which the half-rays of a single ray are completely separated by intersecundibrachs (text-fig. 2a–f, h). 2, areas in which intersecundibrachs are absent and the brachials of the two half-rays are joined together; and 3, areas which are intermediate between the two above types (text-fig. 2g). Most intersecundibrachial areas are complete although several examples of the other two types are known. The nature of the intersecundibrachs is correlated with the amount of fusion of the inner arms. Fully developed intersecundibrachial areas comprise a primitive character in melocrinitids such as *Glyptocrinus*, *Alisocrinus*, and most specimens of *Promelocrinus*. In these forms the inner arms are not fused together. Most advanced melocrinitids, for example, *Ctenocrinus* and *Melocrinites*, exhibit intersecundibrachial areas with a reduced number of plates or the intersecundibrachs may be lacking. The inner arms of these crinoids are fused together to form a more or less solid ray trunk which provides strong support for the numerous ramules. Variation of the nature of the intersecundibrachial areas of *P. anglicus* is not surprising because the species is a large crinoid with numerous ramules which occupies an evolutionary intermediate position between *Alisocrinus* and *Ctenocrinus* (see Ubaghs 1958; Brower 1973) for evolution of melocrinitids). Tables 3 and 4 list the statistics for variation in the intersecundibrachs. As in the case of the interbrachs, all of the parameters for variation of the number of plates in the different ranges are positively correlated. From proximal to distal ranges, the average number of plates per range varies from 0·96 to 1·8, and the percentage standard deviations are also augmented from 20 to 71%. Comparison of Tables 1 and 3 shows that the percentage standard deviations for the intersecundibrachs

are much larger than those of the interbrachs. Thus *P. anglicus* follows the pattern of variation seen in most Palaeozoic camerates with many fixed-brachials in that the more distal intersecundibrachs are more variable than the more proximally located interbrachs. The distribution of correlation coefficients for the different ranges of intersecundibrachs parallels that for the interbrachs except that the correlation coefficients are significant for the number of plates in almost all ranges except the most distal one. However, the number of plates in a given range is most highly correlated with the number of plates in the adjacent ranges and the degree of correlation decreases with more distant ranges. The difference in correlations between the interbrachs and the intersecundibrachs is probably because the secundibrachs are found in a more restricted and constricted area than the interbrachs. The data for the inter-tertibrachs are similar to those of the intersecundibrachs.

TABLE 3. Table showing variation of intersecundibrachs.

Number of range (numbers increase from proximal to distal ranges of plates)	Mean number of intersecundi-brachs in listed range	Standard deviation	Percentage standard deviation [(standard deviation/ mean) × 100]	Range	Number of specimens
1	0·963	0·193	20·0	0·0–1·0	27
2	1·07	0·385	35·8	0·0–2·0	27
3	1·07	0·567	52·8	0·0–2·0	27
4	1·19	0·503	42·4	0·0–2·5	27
5	1·23	0·491	39·9	0·0–2·0	25
6	1·24	0·650	52·4	0·0–2·0	24
7	1·42	0·590	39·4	0·0–2·0	21
8	1·81	1·29	71·0	0·0–6·0	17

A matrix of correlation coefficients for the number of plates of all ranges in all interbrachial areas shows that most of these correlations are not significant, which indicates that much variation between the different interbrachial areas is independent. There are two general areas of significant correlation. The number of inter-secundibrachs is inversely correlated with the number of interbrachs in the fourth range. These coefficients range from -0.54 to -0.75. This is geometrically reasonable because the fourth range of interbrachs occurs at the proximal secundibrach level which is where the intersecundibrachs begin. Basically many crinoids with numerous interbrachs in the fourth range have relatively wide interbrachial areas at this level; this constricts the rays and results in a reduced number of intersecundi-brachs. The reverse is observed for crinoids which show relatively small numbers of interbrachs in the fourth range in conjunction with a high number of intersecundi-brachs (see text-fig. 2). Although many of the coefficients are not significant, the number of intertertibrachs is generally positively correlated with the number of intersecundibrachs (correlation coefficients range from nil to 0·74).

Summarizing, for a given interbrachial area the number of plates in each range and the variation of number of plates increases distally. The intersecundibrachial and intertertibrachial areas are more variable than the interbrachial areas. The number of plates in a given range is most highly correlated with the number of plates in the

TABLE 4. Correlation matrix for the intersecundibrachs. (All correlation coefficients are significant at the 0·05 risk level; those in italics are also significant at the 0·01 level.)

Position of intersecundibrachial range (numbers increasing distally)	1·00	*0·917*	0·819	0·725
Number of intersecundibrachs in the various ranges	*0·917*	1·00	*0·908*	0·730
Standard deviation for number of plates in the various ranges	0·819	*0·908*	1·00	*0·930*
Percentage standard deviation	0·725	0·730	*0·930*	1·00

adjacent ranges and less well correlated with plates that are further away. The number of plates in the interbrachial, intersecundibrachial, and intertertibrachial areas shows much independent variation. However, the number of intersecundibrachs is somewhat positively correlated with the number of intertertibrachs and the number of intersecundibrachs is inversely related to the number of interbrachs at the secundibrach level.

Variation in arm-branching pattern. The number of brachials was counted at various strategic points, including the number of secundibrachs, tertibrachs, and the brachials separating the various ramules. Up to 162 rays could be seen in fifty-one specimens. It is not possible to compile complete sets of data for several reasons. Almost all crinoids are preserved on slabs and some of the rays cannot be determined because they are buried in matrix. Anywhere from one to ten half-rays could be measured on individual specimens. Most visible rays are not complete and the distal tips of the arms are missing. In smaller specimens the arms have not fully developed (see later discussion of ontogeny), and the higher brachials and ramules had not formed when these individuals died. Thus most information is derived from the proximal part of the arms.

In the first step of the analysis, variation within the arms of single specimens was investigated relative to variation between specimens. F-ratios indicate that there is no significant difference in variation patterns within and between the specimens. Consequently, all subsequent discussion will only treat variation between specimens. Each data point comprises the average number of secundibrachs, etc., for a single crinoid. The following general trends are noted in the statistics of Table 5. The percentage standard deviations (i.e. (standard deviation/mean) $\times$ 100) range from 8·9 to 16·7%. These values are roughly similar to those of many camerate crinoids (e.g. systematic descriptions of Brower 1973). The mean number of secundibrachs is 2·08. Almost all crinoids have two secundibrachs; most variant half-rays are characterized by three plates. If three plates are present, these are shorter than those of the normal half-rays with two plates. The average number of tertibrachs comprises 5·99 plates and the number varies from five to seven plates. Within a single crinoid, the total number of secundibrachs and tertibrachs is generally constant or almost so. In a half-ray with an extra secundibrach, the tertibrachial series usually possesses one less plate than the normal neighbouring half-rays. The result of this pattern is that the proximal ramule of the adjacent half-rays occurs at the same level. This is necessary to ensure that each half-ray develops equally and filters the same amount of water.

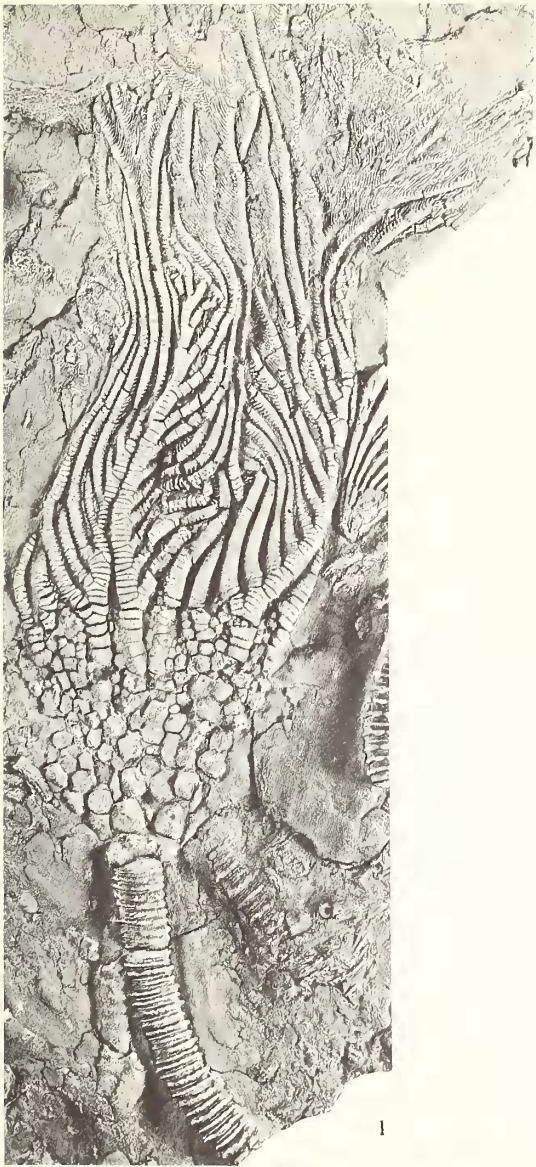TABLE 5. Table showing variation of arm-branching pattern.

Parameter	Mean	Standard deviation	Percentage standard deviation [(standard deviation/mean) × 100]	Range	Number of specimens
Number of secundibrachials	2·09	0·297	14·2	1·0–2·5	51
Number of tertibrachials	5·99	0·532	8·89	5·0–7·0	50
Number of brachials between listed ramules					
1 and 2	4·23	0·500	11·8	3·0–5·0	51
2 and 3	4·62	0·632	13·7	3·0–6·0	49
3 and 4	5·02	0·674	13·4	4·0–7·0	45
4 and 5	5·22	0·668	12·8	4·0–6·5	37
5 and 6	5·18	0·611	11·8	4·0–6·0	31
6 and 7	5·20	0·705	13·6	4·0–7·0	27
7 and 8	5·13	0·830	16·2	3·5–6·0	20
8 and 9	4·93	0·720	14·6	3·5–6·0	16
9 and 10	5·39	0·858	15·9	4·0–7·0	9
10 and 11	6·06	0·943	15·6	5·0–8·0	8
11 and 12	5·4	0·548	10·1	5·0–6·0	5
12 and 13	5·8	0·837	14·4	5·0–7·0	5
13 and 14	6·0	1·000	16·7	5·0–7·0	3

Turning to parts of the arms which bear the ramules, the average number of brachials separating the adjacent ramules ranges from 4·23 to 6·06 as listed in Table 5. The relationships between ramule position, number of plates between the adjacent ramules, the standard deviations, and the percentage standard deviations are given by the correlation matrix in Table 6. Inspection of the correlation matrix shows that the number of plates separating the ramules, the standard deviations, and the position of the ramules are all positively correlated at the 0·01 risk level. The average number of plates and the variation of number of plates increases proceeding from proximal to distal parts of the arms. This general pattern is common in many Palaeozoic crinoids (e.g. systematic descriptions in Brower 1973). The percentage standard deviations which show relative dispersion are not significantly correlated with position of the ramules or average number of plates although the correlation between standard deviation and percentage standard deviation is significant.
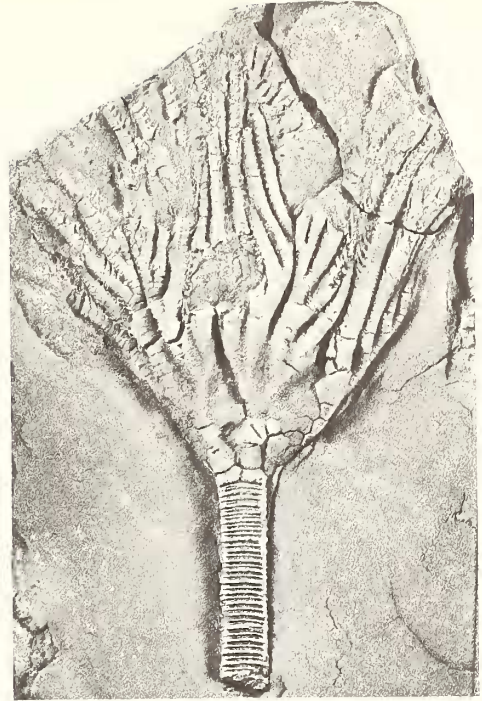
A correlation matrix was also calculated for numbers of plates between the ramules. Several of these correlations are significant at the 0·05 and 0·01 levels, namely those involving plates in the middle of the arms ranging from above the fourth ramule to below the eighth ramule. These correlations range from 0·49 to 0·67. Within this

PLATE 100

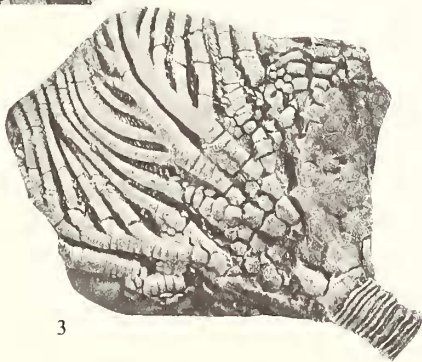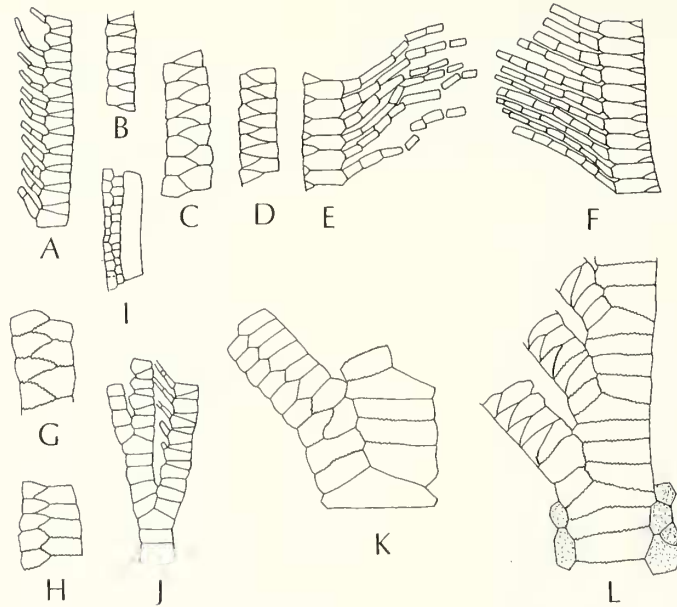TEXT-FIG. 3. *Promelocrinus anglicus* Jaekel. A–H, ramule and outer arm fragments, ×7·0; A, side view of uniserial brachials, BMNH. E26498; B, side view of immature biserial brachials, BMNH. 38648; C and D, front views of immature biserial brachials, S. 270 and GSM. 85098 respectively; E and F, side views of immature biserial brachials with complete or nearly complete pinnules, S. 271 and GSM. 85098 respectively; G and H, front views of immature biserial brachials showing crenulate sutures, GSM. 85098 and 91770 respectively. I, ventral view of pinnular with covering plates, GSM. 85098, ×28·0. J–L, fragments of ray trunks and associated ramules; J, second and third ramules of BMNH. E26498, an immature specimen, note uniserial brachials of ramule and small number of ramule brachials which are joined to the adjacent ray trunks, ×7·0; K, first ramule of SM. A10136, a large adult in which numerous ramule brachials are joined to the adjacent part of the ray trunks, the ramule has mature biserial brachials, crenulate sutures are well developed, ×7·0; L, first through third ramules of SM. A12767, an adult crown, ray trunk fragment similar to the previous figure except for immature biserial brachials in the ramules, ×5·5. Interbrachials are stippled in L.

interval, a given number of brachials is positively correlated with the number of plates separating the adjacent pairs of ramules. Apart from this, the correlation coefficients are not significant, indicating that these parameters largely vary independently of one another. This is despite the fact that the number of brachials separating the ramules tends to increase distally.

Once the ramules have formed, the number of plates between the adjacent ramules is fixed. All new brachials form at the distal tips of the arms or ramules and no new plates are intercalated between those previously present. There is no significant

TABLE 6. Correlation matrix indicating relationships between the various ramule spacing parameters. (Correlation coefficients which are significant at the 0·01 and 0·05 risk levels are in italics.)

Position of ramules (numbers increasing distally)	1·00	*0·861*	*0·688*	0·411
Number of plates separating adjacent ramules	*0·861*	1·00	*0·790*	0·459
Standard deviation	*0·688*	*0·790*	1·00	*0·905*
Percentage standard deviation	0·411	0·459	*0·905*	1·00

correlation between these counts of brachials and the age or size of the crinoid. In other words, these characters are constant regardless of size of the animal. Consequently it is concluded that these were not subject to natural selection which operated over the observed ontogeny of the species.

Nomenclature. As indicated by Ubaghs (1958, p. 267) the nomenclature has been confusing in the past, notably by *Mariacrinus flabellatus* Salter, 1873 which is a *nomen nudum* (and later put into *Melocrinus* by Woods 1891).

Comparison. Promelocrinus anglicus differs from *P. fulminatus* (Angelin) (see Ubaghs 1958) and *P. radiatus* (Angelin, 1878) (see Ubaghs 1958) from the Wenlock of Sweden as follows: 1, the Swedish specimens are much smaller (calyx height ranges from 6 mm to about 18 mm), whereas adult specimens of *P. anglicus* exhibit calyx heights up to approximately 42 mm. 2, *P. fulminatus* and *P. radiatus* bear one or two ramules in each half-ray whereas equivalent-sized individuals of *P. anglicus* possess four, five, or more ramules. Adults of *P. anglicus* are characterized by twelve to fifteen ramules. 3, the Swedish crinoids have stellate ridges on the interbrachs which are lacking on typical examples of *P. anglicus*. 4, in *P. fulminatus*, nodes occur on the side of the brachials with the pinnule facets but the brachials of *P. anglicus* are comparatively smooth. 5, the brachials in the ramules and outer arms of *P. radiatus* are uniserial but immature biserial brachials are found in equivalent-sized specimens of *P. anglicus* (calyx height roughly 18 mm). However, both *P. fulminatus* and young specimens of *P. anglicus* (calyx height approximately 7 mm) show uniserial brachials.

    P. anglicus has been confused with *Ctenocrinus spectabilis* (Angelin, 1878) (see Ubaghs 1958) from the Silurian of Sweden by Springer (1926) and Bassler and Moodey (1943, p. 559). The ctenocrinid differs in several features. The proximal parts of the ray trunks of the ctenocrinid are fused whereas those of *P. anglicus* are separate. In *C. spectabilis* the ramules of the ray trunk are usually separated by six or seven plates in contrast to the four to six plates of *P. anglicus*. The lectotype of *C. spectabilis* is characterized by a calyx height of around 15 mm and uniserial brachials. Immature biserial brachials are present in juvenile crowns of *P. anglicus* which are about the same size.

<center>*Promelocrinus* sp.</center>

<center>Text-fig. 4</center>

    1958   *Promelocrinus* sp., Ubaghs, p. 299, text-fig. 17*a*.
    1973   *Promelocrinus* sp., Webster, p. 225.

Locality. Silurian, Wenlock. Dudley Limestone, near Dudley, West Midlands, probably Wrens Nest Inlier.

Remarks. This form is represented only by a single specimen in matrix showing parts of two rays (BMNH. 57137). Unlike most specimens, the arms are preserved in the outstretched or food-gathering position. The nature of the ray trunks indicates assignment to *Promelocrinus* with no doubt. The presence of at least seven ramules in conjunction with ray trunk arms or inner arms that are not fused together is diagnostic even though the dorsal cup is unknown. Other melocrinitids, such as *Ctenocrinus*,

TEXT-FIG. 4. *Promelocrinus* sp. Dorsal view of BMNH. 57137, the arms are preserved in food-gathering orientation, ×1·9.

with well-developed ray trunks are characterized by inner arms which are wholly or partially fused together (for example, see Ubaghs 1958, pp. 279, 293–304). *Lamptero-crinus*, a dicyclic crinoid with ray trunks, has only one ray trunk arm per ray in contrast to the two ray trunk arms in each ray of *Promelocrinus* (see Springer 1926). *Promelocrinus* sp. is not conspecific with either *P. anglicus* or *P. fulminatus* (Angelin) (see Ubaghs 1958) from the Wenlock of Gotland, which has one ramule whereas the English form has at least seven ramules. In addition, *P. fulminatus* has nodose brachials on the ray trunk which are more massive and wider relative to height than the non-nodose brachials of this crinoid. In *P. anglicus*, crinoids bearing ray trunks of this size are characterized by ramules and outer arms with biserial brachials in contrast to the uniserial brachials of *Promelocrinus* sp. This crinoid is most closely related to *P. radiatus* (Angelin) (see Ubaghs 1958) which is also found in the Wenlock of Gotland. Unfortunately, *P. radiatus* cannot be completely characterized because the arms are not fully known except in one immature specimen. *Promelocrinus* sp. and

EXPLANATION OF PLATE 101

Adult specimens of *Promelocrinus anglicus* Jaekel. 1, *D* ray view of S. 270, crown figured by Springer (1926, pl. 5, fig. 3) as *Melocrinus? spectabilis* Angelin, note broken base which was restored in Springer's figure, the specimen is weathered so that the calyx plates seem smooth. 2, *C* ray view of SM. A10136, syntype of *Mariacrinus flabellatus* Salter, a weathered specimen with median-ray ridges and finely granulose calyx plates, intersecundibrachial areas are incompletely developed. 3, lateral view of GSM. 85098, a partial crown with ornamentation like that of fig. 2, intersecundibrachial areas are complete. 4, *C* ray view of GSM. 91770, a crown which was buried with the arms partially spread, note slightly swollen calyx plates with granulose surfaces and complete intersecundibrachial areas. All figures ×1·5.

PLATE 101
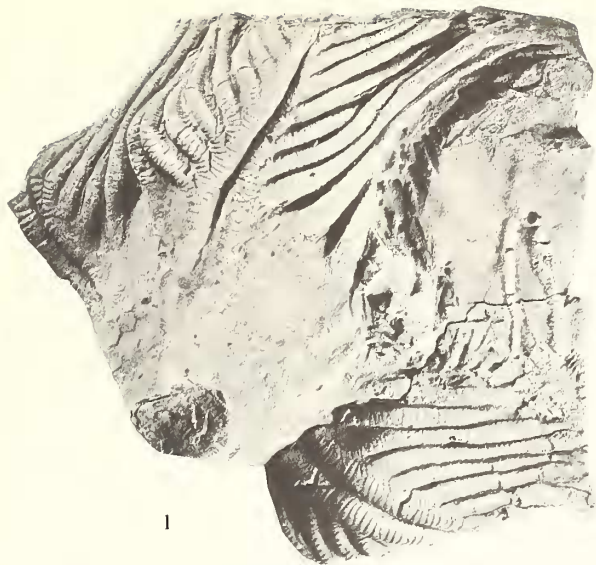
BROWER, Wenlock crinoids

P. radiatus resemble each other in having relatively high uniserial brachials through-out the arms and the two crinoids might belong to the same species. However, this cannot be definitely determined until adult specimens of *P. radiatus* with reasonably complete ray trunks have been found.

ONTOGENY OF *PROMELOCRINUS ANGLICUS*

Ontogeny and phylogeny are intimately related in melocrinitids because the group evolved through 'mutations' (used in most general sense, to include gene changes, chromosome additions, deletions, etc.) which affected the ontogeny of young crinoids by causing divergences that were accentuated throughout subsequent development (Ubaghs 1958, pp. 293-304; Brower 1973, pp. 328-331, 432-437). Reasonably complete ontogenetic sequences are available for several species in the lineage, namely *Glyptocrinus decadactylus* Hall of the Upper Ordovician (see Wachsmuth and Springer 1897 for drawings of adults; young specimens have never been illustrated) and *Alisocrinus tetrarmatus* Brower of the Upper Ordovician (Brower 1973), both of which are primitive forms lacking ray trunks; *P. anglicus* of the Wenlock, a moderately advanced form; and *Ctenocrinus paucidactylus* (Hall) of the Lower Devonian (Goldring 1923; Brower 1974), an advanced ctenocrinid. The most interesting aspect of *P. anglicus* is the development of the food-gathering system and its comparative ontogeny with that of other crinoids. The following measurements have been made on the thirteen crinoids in the growth sequence. 1, 'size' which is height from the base of the calyx to the distal margin of the primaxil. This is the standard measure of relative age in camerate crinoids. Larger crinoids are considered chronologically older than smaller ones. 2, calyx height. Measured from the base of the calyx to the distal intersecundibrach. 3, distal fixed-brachial in the intersecundibrachial areas. For statistical purposes, this character is coded in a numerical scale in which the proximal and distal margins of tertibrach *2* are assigned values of 14 and 15, respectively, and so on. 4, calyx width. Measured from the centre of two adjacent rays at the level of the primaxil. 5, number of ramules in a half-ray. 6, length of and number of plates in the ray trunk (the initial part of the ray trunk begins at the proximal tertibrach). 7, length of and number of brachials in the free parts of the outer arms. 8, length of and number of brachials in the average ramule. All complete ramules on one individual are measured and the average determined. 9, length of and number of pinnulars in the average pinnule. A reasonable number of complete pinnules is used to estimate the average. 10, length of and number of plates in the entire food-gathering system (see later discussion for formulae).

The basic statistics derive from the simple power function or allometric equation $Y = b . X^k$ (Huxley 1932 and Gould 1966, for derivation and discussion of the equation), in which X and Y are the independent and dependent variables, respectively. A reduced major axis procedure (Imbrie 1956; Hayami and Matsukuma 1970) was selected for fitting the equations rather than the least squares method (Sokal and Rohlf 1969). This technique has the advantage of yielding slopes which are not biased by the choice of independent and dependent variables.

Growth of the calyx. As in most crinoids with many fixed-brachs, new brachials were incorporated into the calyx throughout ontogeny although the rate of fixation is most rapid in the youngest animals and declines with increasing 'size' and age (equation 1, Table 7). The smallest crinoids ('size' 5·5 mm) have tertibrach *3* joined into the calyx (text-fig. 2*e*, *h*). When a 'size' of 12–14 mm was attained, the highest fixed-brach ranges from tertibrach *6* to *10* (text-fig. 2*a*, *b*, *d*, *f*, *g*). Tertibrach *10* forms the highest fixed-brach in the largest crinoid, 'size' 20·5 mm. The nature of brachial fixation is similar to that of most camerate crinoids (see Brower 1973, p. 310; 1974, p. 14). Before incorporation into the calyx, the brachials and pinnulars resemble the higher free brachials and pinnulars. During and soon after fixation into the calyx, these plates develop angular margins along which the interbrachs, intersecundibrachs, etc., join them into the cup. The formation of these angular margins involves complex changes in the various width growth rates of the brachials and pinnulars. The fixed-brachs are differentiated from the interbrachs throughout ontogeny by larger size and the presence of median-ray ridges. To a lesser extent, the same is true of fixed-pinnulars during the early stages of incorporation; however, these differentiating features gradually disappear throughout subsequent ontogeny and eventually the pinnulars cannot be separated from the surrounding interbrachs. The origin of the fixing interbrachs is uncertain but these probably represent interambulacrals of the tegmen which become incorporated into the calyx (Brower 1973, 1974).

The calyx height is augmented throughout ontogeny during which the calyx height grows slightly more rapidly than one would predict based on ideal geometry (equation 2, Table 7). Two processes are involved in the development of calyx height, namely the incorporation of new plates into the calyx and the height growth rates of old plates. The ontogeny of calyx width relative to 'size' is isometric (equation 3, Table 7). All growth of calyx width represents calcite accretion on to previously present plates and new plates were not intercalated between old ones during ontogeny.

TABLE 7. Table giving equations for growth of calyx and components of the food-gathering system relative to 'size' in *Promelocrinus anglicus*. Independent variable for all equations is 'size'. 'Sizes' of smallest and largest crinoids are 5·5 and 20·5 mm. The ideal exponent equals 1·0 for all equations.

Equation number	Dependent variable (y)	Initial intercept	Exponent	Predicted minimum Y	Predicted maximum Y	Correlation coefficient	Standard error for slope
1	Distal fixed-brach in intersecundibrachial areas	7·62	0·447	16·3	29·4	0·981	0·0241
2	Calyx height mm	1·66	1·07	10·3	42·1	0·970	0·0716
3	Calyx width mm	1·36	0·998	7·44	27·6	0·955	0·0820
4	Brachials in outer arm	13·6	1·25	115·0	596·0	0·930	0·127
5	Length of outer arm mm	3·12	1·22	25·2	126·0	0·942	0·114
6	Brachials in ray trunk	2·67	1·18	20·0	94·8	0·925	0·124
7	Length of ray trunk mm	0·983	1·39	10·6	65·9	0·950	0·121
8	Number of ramules	0·614	1·11	4·07	17·5	0·938	0·107
9	Number of brachials in average ramule	11·3	1·19	86·4	414·0	0·911	0·137
10	Length of average ramule mm	2·63	1·16	19·0	87·2	0·926	0·121

Ontogeny of components of the food-gathering system. The earliest growth stages of the food-gathering system are unknown and the youngest crinoids, 'size' 5·5 mm, possess juvenile ray trunks with four ramules and half-rays containing 200–500 brachials (text-fig. 2e, f; Pl. 100, figs. 2, 4). The largest crinoids exhibit 'sizes' of around 20·5 mm and complex food-gathering systems in which the ray trunks bear up to fifteen ramules and about 5500 brachials in a half-ray (see Pl. 100, fig. 1; Pl. 102, fig. 2 for nearly complete crowns of large adults). The equation data for development of the components of the food-gathering system (Y or dependent variable) relative to 'size' (X or independent variable) are listed in Table 7. In all cases, the ideal exponent equals 1·0 because both variables are linear dimensions. Note that the observed exponents all exceed the ideal value, although in some instances the differences are not statistically significant. This indicates that the components of the food-gathering system grow more rapidly with respect to size of the calyx than one would predict based on ideal geometrical considerations. In other words, growth of these parameters is subject to positive allometry.

The outer arms remain unbranched and these constitute a subordinate part of the food-gathering system throughout ontogeny while the inner arms gradually become hypertrophied into highly ramified ray trunks which dominate the entire food-gathering system. The growth of the outer arms follows the pattern established in ancestral glyptocrinids with four arms in each ray such as *Alisocrinus tetrarmatus* (see Brower 1973). New brachials form at the distal tips of the arms (equation 4, Table 7). Young crinoids have outer arms with roughly 130 brachials while adults are characterized by about 460 plates. Largely due to the addition of new plates, the length of the outer arms rises from about 30 mm to a maximum of 113 mm (equation 5, Table 7). Growth of the outer arms is similar to the ramules as discussed later.

New brachials are added to the ray trunk throughout life (equation 6, Table 7). All embryonic plates form at the distal tips of the ray trunks and new plates are not intercalated between those previously present. All plates in a ray trunk are uniserial, either being axillary to ramules and higher brachials of the ray trunk or uniserial and nonpinnulate. The smallest crinoids show about twenty brachials in the ray trunk whereas roughly seventy-five brachials are present in the largest specimens. The length of the ray trunks rises throughout ontogeny due to the addition of new plates
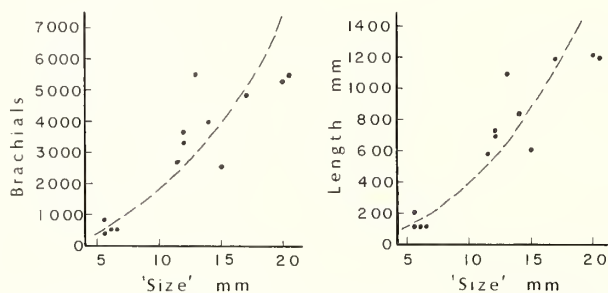
TEXT-FIG. 5. Graphs showing the ontogeny of the length and number of brachials in a half-ray relative to 'size' for *Promelocrinus anglicus* Jaekel.

as just mentioned and increasing height of the previously formed plates (equation 7, Table 7). The ray trunks of the youngest and oldest crinoids are about 11 mm and 55 mm long respectively. The distal tips of the ray trunks are only known in several specimens in which these consist of four or five small brachials that are uniserial and nonpinnulate (see Ubaghs 1958, text-fig. 17*c*–*e*).

New ramules form throughout the observed ontogeny and four or five ramules occur in the youngest crinoids but mature adults ('size' 17·0–20·5 mm) may have anywhere from twelve to fifteen ramules (equation 8, Table 7). Although some variation in number of ramules exists in mature crinoids, there is no indication that various individuals attain a certain number of ramules after which new ones cease to develop. As far as can be determined, the crinoids continue to initiate new ramules throughout ontogeny. Both the number of brachials in and the length of the average ramule continue to increase during the observed ontogeny (equations 9, 10, Table 7). All new plates first appear at the distal tip of the ramule. The ramules of young crinoids are characterized by 70–130 brachials and lengths varying from 17 to 30 mm. The same figures for adults comprise about 350 brachials and 75 mm. As in the ray trunks, two processes interact to increase the length of a ramule, namely the rate of supply of new plates at the distal tips of the ramules and the rate of height growth of old plates. The dominant factor is the plate supply rate. This is shown by the fact that the height of the average brachials in the ramules ranges from 0·19 to 0·25 mm regardless of age. However, some increase in ramule length represents changes in height of the component plates because brachials of the same ramule do become higher throughout ontogeny. For example, the proximal brachials of the first ramule have heights of about 0·5 mm in the smallest crinoids and 0·7 mm in the largest. These data demonstrate that most height increase of brachials takes place early during ontogeny of the plates as in other camerates studied by Brower (1973).

During ontogeny the brachials of the ramules and outer arms undergo systematic changes. All brachials are pinnulate except for a few of the proximal plates. Some of the smallest specimens exhibit uniserial brachials; most larger crinoids have immature biserial brachials and a few of the largest specimens possess mature biserial brachials in the proximal parts of the ramules. Several features can be related to problems of supporting the growing arms and ramules. In small specimens, only one or two of the proximal brachials in a ramule are joined to the adjacent plates of the ray trunks. As the ramules become longer and heavier, several more of the proximal brachials in the ramule are fused to the ray trunk to better support the ramules. The ray-trunk brachials of young crinoids are comparatively slender and graceful but those of mature crinoids are much wider and heavier—apparently in response to a need for better support (compare crinoids in text-fig. 3). Unlike more advanced melocrinitids such as *Ctenocrinus paucidactylus* (Hall), the inner arms of *Promelocrinus anglicus* do not fuse together to provide better support for the arms.

Table 8 lists data for the development of the number of brachials and length of the arms in a half-ray for *P. anglicus* and various other species. If the reader wishes to visualize the total number of brachials and the entire length of the arms, then the half-ray figures and the initial intercepts of the equations should be multiplied by 10·0 because each crinoid has ten half-rays. All variables, 'size', length of half-ray, and brachials in a half-ray are linear dimensions so the ideal exponent is 1·0. The

TABLE 8. Table giving equations for development of the arms in a half-ray relative to 'size' for *Promelocrinus anglicus* and other crinoids. Independent variable for all equations is 'size'. Equations 1–4 were fitted by the reduced major axis method whereas 5–16 were computed by least squares. However, the correlation coefficients are high enough so the equations fitted by both techniques can be compared with little loss of information.

Equation number	Species	Dependent variable (y)	Initial intercept	Exponent	Minimum 'size' (x) mm	Predicted minimum y	Maximum 'size' (x) mm	Predicted maximum y	Correlation coefficient	Standard error for slope
1	*Promelocrinus anglicus*	Brachials per half-ray	14·1	2·09	5·5	496·0	20·5	7730·0	0·934	0·207
2	*Promelocrinus anglicus*	Length of half-ray mm	3·78	2·02	5·5	117·0	20·5	1660·0	0·946	0·182
3	All melocrinitids	Brachials per half-ray	2·12	2·22	4·0	46·3	28·0	3500·0	0·631	0·310
4	All melocrinitids	Length of half-ray mm	2·03	1·91	4·0	28·5	28·0	1180·0	0·730	0·234
5	*Alisocrinus tetrarmatus*	Brachials per half-ray	9·38	1·49	1·1	10·80	6·7	160·0	0·978	0·0994
6	*Alisocrinus tetrarmatus*	Length of half-ray mm	2·12	1·73	1·1	2·50	6·7	57·6	0·970	0·138
7	*Eopatelliocrinus scyphogracilis*	Brachials per half-ray	7·38	1·10	1·15	8·60	7·7	70·0	0·893	0·148
8	*Eopatelliocrinus scyphogracilis*	Length of half-ray mm	1·91	1·35	1·15	2·31	7·7	30·0	0·945	0·124
9	*Eopatelliocrinus latibrachiatus*	Brachials per half-ray	8·21	1·29	1·15	9·82	5·0	65·1	0·916	0·199
10	*Eopatelliocrinus latibrachiatus*	Length of half-ray mm	1·76	1·52	1·15	2·17	5·0	20·4	0·935	0·205
11	*Macrostylocrinus pristinus*	Brachials per half-ray	6·60	1·47	1·0	6·60	7·0	116·0	0·952	0·136
12	*Macrostylocrinus pristinus*	Length of half-ray mm	1·47	1·47	1·0	1·47	7·0	36·2	0·964	0·161
13	*Ptychocrinus splendens*	Brachials per half-ray	6·32	1·53	2·1	19·7	12·7	312·0	0·931	0·161
14	*Ptychocrinus splendens*	Length of half-ray mm	1·52	1·74	2·1	5·50	12·7	126·0	0·948	0·156
15	*Ptychocrinus fimbriatus*	Brachials per half-ray	9·69	0·784	2·3	18·6	7·5	47·0	0·960	0·114
16	*Ptychocrinus fimbriatus*	Length of half-ray mm	3·48	0·674	2·3	6·11	7·5	13·6	0·977	0·073

earliest specimens of *P. anglicus* probably have four equal-sized arms in a ray in which pinnules are present in the two outer arms but lacking in the two inner arms. During later ontogeny the outer arms remain unbranched although new brachials form and the length of the arms increases. The inner arms gradually become hypertrophied into highly ramified ray trunks. The length of the ray trunk is augmented throughout ontogeny by growth of new brachials and height increase of old plates. As new brachials are added to the ray trunk, new ramules are initiated. Once the ramules appear, new brachials appear at the distal tips of the growing ramules. Young crinoids have half-rays which are 100–200 mm long with about 400–800 brachials. In mature crinoids, up to 5500 brachials may be present in half-rays in which the arms are up to 1200 mm long (text-fig. 5). The equations for development of the arms in *P. anglicus* are (equations 1, 2, Table 8).

$$\text{(Length of arms)} = 3 \cdot 78 \, (\text{'size'})^{2 \cdot 02}$$
$$\text{(Number of brachials)} = 14 \cdot 1 \, (\text{'size'})^{2 \cdot 09}$$

In both cases the ideal exponent is 1·0 whereas the observed exponents are 2·02 and 2·09. The implication is that the development of the type of ray trunks seen in *P. anglicus* and other melocrinitids roughly squares the rate of increase of number of brachials and length of the arms relative to idealized crinoids. The *P. anglicus* figures are similar to the equations calculated in a preliminary study of evolution of melocrinitids and allied forms. The data are derived from adult crinoids of thirty-one species ranging from middle Ordovician to upper Devonian in age (equations 3, 4, Table 8). General discussions of the evolution of melocrinitids are available in Ubaghs (1958) and Brower (1973). The most primitive crinoid in the sequence, *Glyptocrinus ornatus* Billings of the middle Ordovician (Wachsmuth and Springer 1897), has only two unbranched arms in each ray. The next step in evolution of melocrinitids is the acquisition of four arms in each ray as seen in the upper Ordovician *Alisocrinus tetrarmatus* Brower. Throughout later evolution, the inner arms gradually became hypertrophied into extensively ramified ray trunks which completely filtered the water surrounding the crinoid. The primitive species of *Promelocrinus* from the Silurian of Gotland, *P. fulminatus* (Angelin) (see Ubaghs 1958) and *P. radiatus* (Angelin) (see Ubaghs 1958), have only a few ramules but some advanced species of *Melocrinites* exhibit up to thirty or thirty-five ramules in a half-ray, for example, the Devonian species *M. acicularis* Follmann (Schmidt 1941), *M. malcontractus* (Schmidt 1934), and *M. clarkei* Williams (see Goldring 1923). Concomitant with the evolution of the ray trunks, the outer arms of a ray are gradually reduced and eventually lost. This is necessary to provide space for the proximal ramules of the ray trunks. One upper Devonian genus, *Trichotocrinus* (see Goldring 1923), went to the extreme of superimposing accessory ray trunks on the main ray trunks although this seems to have been an unsuccessful evolutionary experiment. At least some of these evolutionary changes are partially reflected in the ontogeny of melocrinitids such as *P. anglicus* and *Ctenocrinus paucidactylus* (Hall). The earliest specimens have four unbranched arms in each ray in which pinnules are lacking on the inner arms. This growth stage is known in *C. paucidactylus* but not in the promelocrinid. A similar phylogenetic stage with four arms in each ray is seen in *A. tetrarmatus* Brower and *G. decadactylus* although both the inner and outer arms bear pinnules. Throughout

F

the ontogeny of *C. paucidactylus* and *P. anglicus*, new ramules are initiated as the ray trunks grow distally. Grossly similar changes are seen in the evolutionary sequence of *Promelocrinus* to *Ctenocrinus* to *Melocrinites*.

Brower (1974, pp. 33–44) discussed comparative ontogenies of camerate crinoids showing various types of brachials and arm-branching patterns, although quantitative data were not then available for forms with ray trunks. Consequently, the contrast between forms with and without ray trunks and hypertrophied arms will be emphasized. Note that both the exponents and the initial intercepts for the equations of *P. anglicus* are larger than those of the other crinoids (compare equations 1, 2 with 5–16 in Table 8). The slowest rates of growth of length of arms and number of brachials are found in the Ordovician *Eopatelliocrinus scyphogracilis* Brower, *E. latibrachiatus* Brower, 1973, and *Ptychocrinus fimbriatus* (Shumard) (see Brower 1973). All of these forms have two unbranched arms in each ray which consist of uniserial pinnulate brachials (equations 7–10, 15, 16, Table 8). Although none of these species are closely related to melocrinitids, the same configuration is seen in the ancestor of the Melocrinitidae, *G. ornatus*.

The acquisition of biserial brachials allows more brachials per unit length of arm because each side of the arm has a column of brachials. *Macrostylocrinus pristinus* Brower, has two unbranched biserial arms per ray which results in a more rapid rate of brachial addition relative to 'size' than seen in the eopatelliocrinids and *P. fimbriatus* (equations 11, 12, Table 8). Most advanced melocrinitids have biserial brachials as in *Promelocrinus anglicus* or compound brachials as found in some species of *Melocrinites* (compound brachials represent several biserial brachials which are fused together).

A. tetrarmatus Brower, a species with four unbranched arms in each ray that are composed of uniserial brachials, lies in the ancestry of *P. anglicus*. Note that the rate of development of new brachials and length of the arms is significantly slower than in *P. anglicus* (equations 5, 6, Table 8). This difference is directly correlated with the presence or absence of ray trunks and hypertrophied arms. *Ptychocrinus splendens* (Miller) (see Brower 1973) is a dicyclic camerate crinoid with uniserial arms which branch twice above the calyx, the branches being located on secundibrachs *13–15* and tertibrachs *30–40*. The half-rays of this form develop more rapidly relative to 'size' than in most camerates but the rate of growth is still slower than in *Promelocrinus anglicus* (equations 13, 14, Table 8).

In summary, the evolution of complexly ramified ray trunks or hypertrophied arms results in unusually rapid rates of development of new brachials and length of the arms. The rate of growth is roughly squared compared to idealized crinoids with simple arm configurations. Considering the food-gathering system only in terms of the arms and brachials is somewhat misleading because most of the plates and length of the food-gathering structures are represented by pinnules. In most camerates, over 95% of the total length of the food-gathering system is found in the pinnules (Brower 1973, 1974). Unfortunately, the length of and number of pinnulars in the average pinnule has only been measured for three specimens of *P. anglicus*; these data should be considered highly tentative and regarded with more than the proverbial grain of salt. Additional pinnules develop as new brachials are incorporated into the ramules and outer arms. Throughout ontogeny, new pinnulars form at the distal tips of the

pinnules and the length of the pinnule is increased by the addition of new plates and calcite accretion on to old plates. The smallest crinoids, 'size' 5·5 mm, exhibit pinnules about 3·5 mm long which consist of about seven plates. The equivalent values for the largest crinoid from which data can be obtained, 'size' 13·7 mm, are 9·5 mm and twenty-three pinnulars. The equations are listed below.

$$\text{(Length of average pinnule)} = 0·508 \, (\text{'size'})^{1·08}$$
$$\text{(Number of pinnulars in average pinnule)} = 0·725 \, (\text{'size'})^{1·30}$$

About all the equations show is that the pinnules develop approximately isometrically with respect to size of the calyx. Brower obtained similar results for six species of Ordovician camerates (Brower 1974, pp. 35–37; Table 6 gives the exponents relative to calyx volume; these should be multiplied by 3·0 to give exponents with respect to a linear dimension such as 'size').

Growth of the entire food-gathering system. The number of plates and the length of the food-gathering system has been calculated for *P. anglicus* (equations 1, 2, Table 9). The data for the arms are taken from all 13 crinoids in the growth sequence. The figures for the pinnules are computed from the equations previously mentioned. The length of and the number of plates in the food-gathering system is a special type of a linear dimension which is in turn a sum and product of several other linear dimensions. The formulae are:

(Total number of plates =
$$BR + BOA + (PP \times BOA) + (NR \times BAR) + (NR \times BAR \times PP)$$
$$\text{(Total length)} = LR + LOA + (BOA \times LP) + (NR \times LAR) + (NR \times BAR \times LP)$$

BR and *LR* are the number of brachials in and length of the ray trunk.
BOA and *LOA* are the number of brachials in and length of the outer arms.
BAR and *LAR* are the number of brachials in and length of the average ramule.
PP and *LP* are the number of pinnulars in and length of the average pinnule.
NR is the number of ramules.

The equation data are given in Table 9 for *P. anglicus* and a series of other species. In this case, the ideal exponent is 1·0 because all variables are linear dimensions. The main functions of the food-gathering system are to provide the viscera with food and to some extent oxygen. The gonads of camerates are presumably housed in the pinnules as in living crinoids. Extant comatulids also use the arms in moving from place to place by means of swimming and/or crawling although this does not seem to have been common in Paleozoic camerates.

The food-gathering capacity of a crinoid is largely controlled by two variables, firstly the number of plates, including both brachials and pinnulars, in the food-gathering system. This determines the number of food-gathering tube-feet (Brower 1973, p. 323; 1974, pp. 37–40). The second variable is the area drained by the food-gathering system which dictates the over-all size of the food-gathering system as well as the spacing of the food-catching tube-feet. Owing to geometrical complexity and preservation of the crinoids, the area usually cannot be measured and the length of the entire food-gathering system is used instead. Such is not unreasonable because the area comprises some function of length.

TABLE 9. Table giving equations for development of the entire food-gathering system relative to 'size' for *Promelocrinus anglicus* and other crinoids. Independent variable for all equations is 'size'. Equations 1 and 2 were fitted by the reduced major axis method whereas the others were done by least squares.

Equation number	Species	Dependent variable (y)	Initial intercept	Exponent	Minimum 'size' (x) mm	Predicted minimum y	Food-gathering ratio for smallest crinoid (y_{eq}/x_{obs})	Maximum 'size' (x) mm	Predicted maximum y	Food-gathering ratio for largest crinoid (y_{eq}/x_{obs})	Correlation coefficient	Standard error for slope
1	*Promelocrinus anglicus*	Total number of plates	14·3	3·26	5·5	37,300·0	6780·0	20·5	2,740,000	133,000·0	0·974	0·207
2	*Promelocrinus anglicus*	Total length in cm	8·49	3·10	5·5	1670·0	304·0	20·5	98,600	3250·0	0·970	0·208
3	*Alisocrinus tetrarmatus*	Total length in cm	5·88	2·88	1·1	7·73	7·03	6·7	1420	211·0	0·981	0·180
4	*Eopatelliocrinus scyphogracilis*	Total length in cm	6·40	2·25	1·15	8·77	7·62	7·7	631	82·0	0·926	0·246
5	*Eopatelliocrinus latibrachiatus*	Total length in cm	7·49	2·35	1·15	10·4	9·04	5·0	328	65·6	0·885	0·437
6	*Macrostylocrinus pristinus*	Total length in cm	4·35	2·98	1·0	4·35	4·35	7·0	1420	204·0	0·959	0·310
7	*Ptychocrinus splendens*	Total length in cm	10·3	2·07	2·1	47·7	22·7	12·7	1980	156·0	0·935	0·209
8	*Ptychocrinus fimbriatus*	Total length in cm	15·8	1·35	2·3	48·9	21·3	7·5	244	32·5	0·901	0·327

Thus crinoids are faced with the basic functional problem of most filter-feeding marine invertebrates. The food-gathering capacity is, at best, an area or (linear dimension)^2 function, but the tissue to be supplied with food is a volume or (linear dimension)^3 function. In *P. anglicus*, 'size' comprises the linear dimension and no attempt was made to estimate the volume of the calyx or tissue. However, the development of calyx volume relative to 'size' in various Palaeozoic camerates closely follows a cubed function (Brower 1973, 1974).

Several tentative conclusions can be drawn from the table (see also discussion in Brower 1973, p. 319; 1974, pp. 33–44).

1. In general crinoids with pinnulate arms seem to have maximized the growth rates of the length and number of plates in the food-gathering system with respect to size and tissue volume as much as possible within the inherent geometrical limits of the food-gathering system. Except for *Ptychocrinus fimbriatus*, the food-gathering system develops much more rapidly than one would predict based on the ideal case (Table 9).

2. Of all crinoids listed in Table 9, *Promelocrinus anglicus* is characterized by the most rapid rate of growth of the food-gathering system. This is dictated by the interaction of the large exponents and high initial intercepts. For example, both *Macrostylocrinus pristinus* and *A. tetrarmatus* are characterized by large exponents which are only slightly less than in the promelocrinid; however, the initial intercepts of these two species are significantly smaller than in *P. anglicus* which dictates a slower rate of growth of the food-gathering system. In most of the other species, the exponents are much lower than those of *P. anglicus*. This situation is attributed to the acquisition of ray trunks and hypertrophied arms. None of the other species exhibit hypertrophied arms; all have normal patterns of arm branching. Brower (1973, pp. 318–324; 1974, pp. 34–40; see also previous material on the arms) presented discussions of ontogeny of all species except *P. anglicus*.

3. The 'food-gathering ratio' equals [(length of food-gathering system) or (number of plates in food-gathering system) or (number of food-catching tube-feet)]/[(calyx volume) or (volume of tissue)]. *P. anglicus* shows isometry or positive allometry of the food-gathering system relative to tissue volume; consequently the food-gathering ratios either increase or remain constant throughout ontogeny (I assume the tissue volume or calyx volume increases roughly as ('size')^3 during growth). All other species which I have investigated, and probably most camerate crinoids, are characterized by more or less striking negative allometry and the food-gathering ratios decline in older and larger crinoids (Table 9 lists data for growth of the food-gathering system relative to 'size' but this is better seen in the equations with respect to calyx volume given by Brower 1973, pp. 319–323; 1974, pp. 37–40, Table 7).

Continuation of this ontogenetic pattern could produce a 'hypothetical crinoid' where the number of food-catching tube-feet is too low and the food-gathering system too short to provide the volume of soft tissues with food. Obviously no crinoid reached this critical limit although some forms may have approached it. Perhaps some ratio of [(length of the food-gathering system)/(tissue volume)] or [(number of food-catching tube-feet)/(tissue volume)] serves as a limit beyond which further

increase of tissue cannot take place. The achievement of isometry or positive allometry in *P. anglicus* circumvents this particular size limitation. This may be partially reflected in the 'sizes' of the largest adults of the species listed in Table 9. *P. anglicus* is by far the largest form, maximum 'size' being 20·5 mm versus 5·0–12·7 mm. I concede that there are alternative explanations for the differences in 'sizes' which may be equally likely (Brower 1973, pp. 325, 326; 1974, pp. 44–46).

The filtration net. To consider *P. anglicus* and other melocrinitids only in the context of the number of food-catching tube-feet is somewhat misleading. Crinoids trap their food by means of filtration nets which are formed by the arms and pinnules. Melocrinitids probably engaged in full mucus net feeding like most adult crinoids of the Recent (Lane and Breimer 1974). Depending on the environment, the filtration net can be orientated in one of two ways (Breimer 1969). In quiet water conditions the food supply consists of a vertical rain of plankton and/or organic detritus. The stem is erect and the arms are spread horizontally to form a collecting bowl. When current or wave action is present, at least part of the food travels parallel to the substrate. The stem is flexed and bent with the current. In this case, the food-gathering system forms a vertically orientated filtration net. Regardless of environment, the basic orientation of the filtration network is at right angles to the direction of food transport.

Text-fig. 6 illustrates schematic plan views of the filtration networks of two crinoids. The most primitive form, *Glyptocrinus ornatus* has ten unbranched arms. The primitive filtration net is incomplete because there are large gaps between the pinnules of adjacent arms and rays. Several specimens of *Promelocrinus* are preserved with the arms in the spread or food-gathering orientation and these individuals allow reconstruction of the filtration net (e.g. text-fig. 4). Typically, the crinoids were buried with the arms in the partially closed (e.g. Pl. 100, fig. 4) or in the fully closed or resting position (e.g. Pl. 100, fig. 1). In *P. anglicus*, the filtration network is complete and covers the entire perimeter of the arms. There are no large spaces between the adjacent arms and pinnules. Here, almost all food particles flowing through the arms and pinnules would be filtered. The pinnules are too long to fit between the ramules and the outer arms; consequently, these must face distally and outward from the plane


EXPLANATION OF PLATE 102

Figs. 1, 2, 4. *Promelocrinus anglicus* Jaekel. 1, lateral view of SM. A12767, note relatively small arms, complete intersecundibrachial areas, granulose calyx plates with raised margins. 2, lateral view of S. 271, a complete crown with fifteen ramules and crushed calyx, ×1·25. 4, stem segment of SM. A10136, a syntype of *Mariacrinus flabellatus* Salter, the stem segment closely resembles those found attached to crowns of *Promelocrinus anglicus* and this specimen is assigned here with little doubt.

Figs. 3, 5. Specimens assigned by Salter to *Mariacrinus flabellatus* for unknown reasons, I have not seen any such material associated with *Promelocrinus anglicus* and these specimens are unidentified here. 3, SM. A12759, cirrus root lying on a bedding plane, apparently the crinoid was uprooted when burial took place, burial was probably rapid and possibly by mudflow, the living orientation of such cirrus roots which have cirri on all sides is with the axis of the stem vertical. 5, SM. A12761, massive distal stem segment or rooting device with cirri.

All figures ×1·5 unless otherwise stated.

PLATE 102
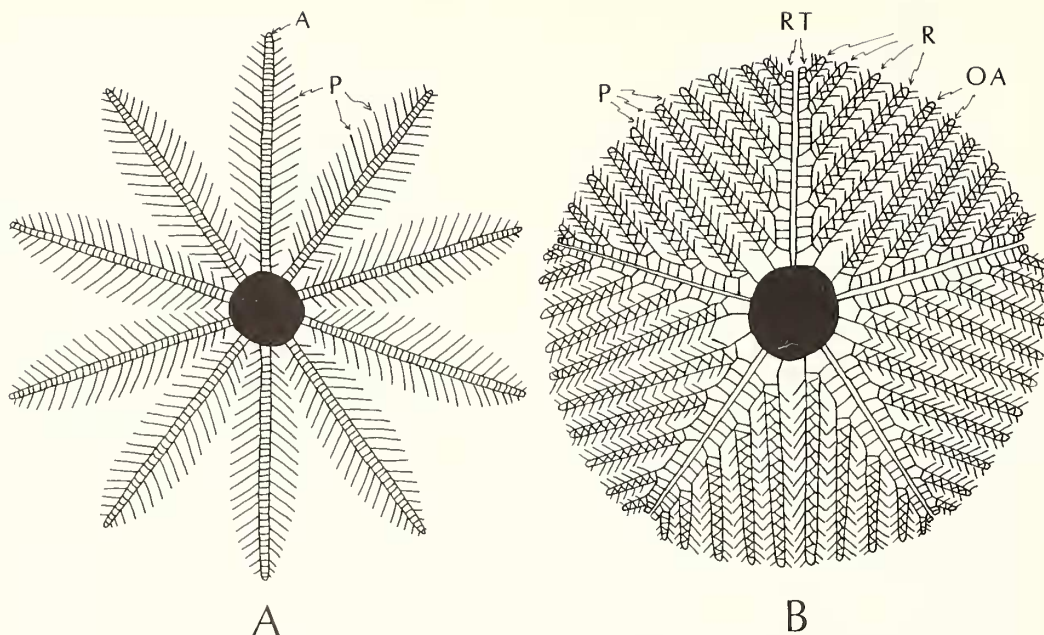
TEXT-FIG. 6. Schematic sketches of plan views for filtration nets of *Promelocrinus* and ancestor, not to any scale. A, *Glyptocrinus ornatus* Billings, note gaps in the filtration net between the arms. B, *Promelocrinus anglicus* Jaekel, the filtration net is complete, only a few ramules are shown in order to simplify the drawing. Symbols: P = pinnules; A = arms in *Glyptocrinus*; RT, R, and OA denote ray trunks, ramules, and outer arms respectively in *Promelocrinus*.

of the arms. One might note that the evolution of ray trunks or hypertrophied arms commonly produces a complete filtration net. This is clearly seen in melocrinitids and in various unrelated crinoids which also developed ray trunks such as *Lamptero-crinus* (see Springer 1926), *Cytidocrinus* (see Wachsmuth and Springer 1897), and *Manillacrinus* (Campbell and Bein 1971).

REFERENCES

ANGELIN, N. P. 1878. *Iconographia crinoideorum in stratis sueciae Siluricus Fossilium*. Holmiae, 62 pp., 29 pls.

BASSLER, R. S. and MOODEY, M. W. 1943. Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms. *Geol. Soc. Am., Spec. Pap.* **45**, 734 pp.

BREIMER, A. 1969. A contribution to the paleoecology of Palaeozoic stalked crinoids. *Koninkl. Nederl. Akad. Wetensch.-Amsterdam, Proc. Ser. B*, **72**, no. 2, 139–150.

BROWER, J. C. 1973. Crinoids from the Girardeau Limestone (Ordovician). *Palaeont. Amer.* **7**, no. 46, 263–499, pls. 59–79, 45 text-figs.

—— 1974. Ontogeny of camerate crinoids. *Univ. Kansas, Paleont. Contrib. Pap.* **72**, 53 pp., 20 figs.

—— In press. Evolution of the Melocrinitidae. *Proceedings volume for second conference on echinoderms, Thalassia Jugoslavica.*

CAMPBELL, K. S. W. and BEIN, J. 1971. Some Lower Carboniferous crinoids from New South Wales. *J. Paleont.* **45**, 3, 419–436, pls. 49–51, 13 text-figs.

CARPENTER, P. H. 1884. Report on the Crinoidea collected during the voyage of H.M.S. Challenger, during the years 1873–1876. Part 1, general morphology, with descriptions of the stalked crinoids. *Challenger Rept., Zool.* **11**, pt. 26, xii + 442 pp., 62 pls., 21 text-figs.

GOLDRING, W. 1923. The Devonian crinoids of the State of New York. *N.Y. St. Mus., Mem.* **16**, 670 pp., 60 pls., 63 figs.

GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev.* **41**, 587–640.

HAYAMI, I. and MATSUKUMA, A. 1970. Variation of bivariate characters from the standpoint of allometry. *Palaeontology*, **13**, 588–605, 12 text-figs.

HUXLEY, J. 1932. *Problems of relative growth*. Methuen & Co., London, 256 pp. (Reprinted by Dover Publ. Inc., 1972.)

IMBRIE, J. 1956. Biometrical methods in the study of invertebrate fossils. *Bull. Amer. Mus. Nat. Hist.* **108**, 215–252.

JAEKEL, O. 1902. Uber Verschiedene Wege Phylogenetischer Entwickelung. *Verh. V. Int. Zool. Cong. Berlin 1901*, 1058–1117 (60 pp.), 28 text-figs.

—— 1918. Phylogenie und System der Pelmatozoen. *Palaeontologischen Zeitschrift, Band* **III**, *Heft.* **1**, 128 pp., 114 figs.

KIRK, E. 1929. The status of the genus *Mariacrinus* Hall. *Am. J. Sci.* **18**, 337–346.

LANE, N. G. and BREIMER, A. 1974. Arm types and feeding habits of Paleozoic crinoids. *Koninkl. Nederl. Akad. Wetensch.-Amsterdam, Proc. Ser. B*, **77**, no. 1, 32–39.

MOORE, R. C. 1952. Crinoids. *In* MOORE, R. C., LALICKER, C. G. and FISCHER, A. G. *Invertebrate fossils*. McGraw-Hill, New York, 604–652, 34 text-figs.

—— and LAUDON, L. R. 1943. Evolution and classification of Paleozoic crinoids. *Geol. Soc. Am. Spec. Pap.* **46**, 167 pp., 14 pls., 18 text-figs.

SALTER, J. W. 1873. *A Catalogue of the Cambrian and Silurian fossils contained in the Geological Museum of the University of Cambridge*. Cambridge Univ. Press, Cambridge, xlvi + 294 pp.

SCHMIDT, W. E. 1934. Die Crinoideen des Rheinischen Devons, I Teil: Die Crinoideen des Hunsrückschiefers. *Preuss. Geol. Landesanst., Abh., n.F.*, Heft **163**, 149 pp., 34 pls., 29 figs.

—— 1941. Die Crinoideen des Rheinischen Devons, II Teil: A. Nachtrag zu: Die Crinoideen des Hunsrückschiefers. B. Die Crinoideen des Unterdevons bis zur *Cultrijugatus*—Zone (mit Ausschluss des Hunsrückschiefers). *Reichsstelle für Bodenforsch., Abh., n.F.*, Heft **182**, 253 pp., 26 pls., 62 text-figs.

SOKAL, R. R. and ROHLF, F. J. 1969. *Biometry*. W. H. Freeman and Co., San Francisco, xxi + 776 pp.

—— 1926. American Silurian crinoids. *Smithson. Inst., Pub.* **2871**, 1–143, 167–239, 33 pls.

UBAGHS, G. 1953. Classe des Crinoïdes. *In* JEAN PIVETEAU (ed.). *Traité de Paléontologie*. Masson et Cie, Paris, 658–773, 166 figs.

—— 1958. Recherches sur les Crinoïdes Camerata du Silurien de Gotland (Suède) Partie III: Melocrinicae, avec des Remarques sur l'évolution des Melocrinidae. *Ark. Zool. Svensk. Vetensk. Akad., ser.* **2**, Bd. **11**, no. **16**, 259–306, 5 pls., 18 text-figs.

WACHSMUTH, C. and SPRINGER, F. 1885–1886. Revision of the Palaeocrinoidea, Pt. III, secs. 1 and 2. *Proc. Acad. Nat. Sci. Philadelphia [for 1885]*, 334 pp. (226–360, 64–227), pls. 4–9.

WACHSMUTH, C. and SPRINGER, F. 1897. The North American Crinoidea Camerata. *Mus. Comp. Zool.,* *Mem.* **20, 21,** 897 pp., 83 pls., 23 text-figs.
WEBSTER, G. D. 1973. Bibliography and index of Paleozoic crinoids 1942–1968. *Geol. Soc. Am. Mem.* **137,** 341 pp.
WOODS, H. 1891. *Catalogue of the Type Fossils in the Woodwardian Museum, Cambridge* with a preface by T. McKenny Hughes. Cambridge Univ. Press, Cambridge, xiv+180 pp.
ZITTEL, K. A. VON. 1878. *Handbuch der Paläontologie, Bd.* I, *Palaozoologie.* München and Leipzig, R. Olden-bourg, Abt. 1, 765 pp., 557 text-figs.

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